Seasonal Dynamics of Nonstructural Carbohydrate Partitioning in 15 Diverse Rice Genotypes

S. O. PB. Samonte,* L. T. Wilson, A. M. McClung, and L. Tarpley

ABSTRACT

The presence of significant variation among rice (*Oryza sativa* L.) genotypes in total nonstructural carbohydrates (TNC) that is related to grain yield should be of interest to rice breeders. The effects of four important yield-determining traits (maximum number of tillers, grain weight, panicle node number, and panicle size) on the TNC concentrations of plant structures at heading and harvest were determined. Path analysis was used to determine the path coefficients of the effect of changes in TNC content (Δ TNC) in leaves or stems on Δ panicle TNC at various stages of crop maturation. Fifteen rice genotypes were used in this study ('Lemont', 'Teqing', and 13 inbred lines obtained from a Lemont × Teqing cross) to represent the combinations of low and high levels of the four important yield determinants. Field experiments were conducted during the 1994 and 1995 cropping seasons at the Texas A&M University Agricultural Research and Extension Center, Beaumont, TX. Path coefficients for the significant direct effects of Δ stem TNC on Δ panicle TNC were −0.46 for the early- to late-heading period and −0.59 for the late-heading to grain hardening period. Significant genotype × developmental stage × plant structure interaction suggested the potential for selection of rice lines with high TNC concentration in stems at heading. Linear contrasts indicated that low-grain weight genotypes had higher stem TNC concentration at harvest, which in turn suggested for the selection of high-grain weight genotypes.

Total nonstructural carbohydrates are sugars, starches, and fructosans that can be accumulated and mobilized for metabolism or translocated to other plant structures (Henjum, 1980; Smith, 1981). For rice, estimates of the contribution by preheading carbohydrates accumulated in vegetative tissues to grain carbohydrates at maturity range from 24 to 27% (Cock and Yoshida, 1972) and 20 to 30% (Murthy, 1976). This contribution is lower at higher levels of fertilizer application and higher for longer-duration cultivars (Yoshida and Aha, 1968, as cited by Murata and Matsushima, 1975). Low temperatures and higher solar radiation tend to increase TNC (Akita, 1995). Preheading carbohydrate storage potentially serves as a buffer to support grain filling during unfavorable weather conditions such as low light intensity (Soga and Nozaki, 1957, as cited by Murata and Matsushima, 1975; Yoshida, 1972).

The TNC present in stems at heading can be a major contributor to grain TNC at harvest (Sato and Inaba, 1976; Weng et al., 1982). However, Akita (1995) emphasized the need to determine the optimum TNC concentration that produces the highest yield, because the presence of TNC beyond a specific limit indicates reduced allocation to structural components in the vegetative organs, which in turn may lead to increased susceptibility to lodging or premature senescence of leaves. The presence of significant variation among rice genotypes in TNC that is related to grain yield is of particular interest to rice breeders (Andrews, 1990). In this study, diverse rice lines obtained from a *japonica* × *indica* cross were studied. The effects of four important yield-determining phenotypic traits (tillering ability, grain weight, panicle node number, panicle size) on the concentrations of TNC in plant structures at heading and at harvest were determined. Path analysis was used to determine the developmental stages during which changes in TNC content in leaves or stems contributed significantly to changes in panicle TNC, and to measure the magnitude of significant direct effect(s) on changes in panicle TNC.

MATERIALS AND METHODS

Field Experiment

The rice genotypes used in this study were Lemont, Teqing, and 14 lines derived from a Lemont × Teqing cross—LQ170, LQ49, LQ55, LQ267, LQ82, LQ348, LQ199, LQ287, LQ125, LQ214, LQ81, LQ338, LQ248, and LQ306 (Li et al., 1995). The LQ lines were F_9 in 1994 and F_{10} in 1995. These recombinant inbred lines were selected from 300 F_8 LQ lines grown in 1993 to represent the combinations of low and high levels of four traits that are important yield determinants—tillering ability, grain weight, panicle node number, and panicle size (Table 1). The basis for the separation between the low and high level genotypes was the population mean for each trait measured from the 300 F_8 LQ lines. Lemont is a tropical *japonica* rice cultivar released in 1983; its characteristics include high yield, high milling percentage, semidwarf stature, and good ratoon potential (Bollich et al., 1985). Teqing is a high tillering, semidwarf *indica* rice cultivar from China with an extremely high yield potential (Wu et al., 1998).

Field experiments were conducted during the 1994 and 1995 summer cropping seasons at the Texas A&M University Beaumont Agricultural Research and Extension Center (29°57′N, 94°30′W). The soil at Beaumont is a fine montmorillonite and thermic Entic Pelludert (Chen et al., 1989). A completely randomized plot design was used with three replicates of each genotype. Each plot was 6 m long and consisted of six rows which were spaced 0.2 m apart. The rice seeds were drill-seeded at the rate of 11.6 g m^{-2} on 20 April 1994, and 15.4 g m^{-2} on 26 April 1995. When the seedlings reached the 3-leaf stage, the plants were thinned to a uniform density of 20 seedlings per meter-row (112 seedlings m^{-2}). In 1994, rice line LQ199 had low seed germination and was thinned to 15 seedlings per meter-row, and line LQ338 had poor germination and was dropped from the study. In both years, fertilizer was applied at planting (34 kg N ha^{-1} in 1994, and 56.7 kg N

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Table 1. Sixteen rice genotypes selected from among recombinant inbred lines of a 'Lemont' × 'Teqing' cross that were analyzed for TNC concentration. High and low levels were separated on the basis of the means estimated from the F_8 generation.

		Tillering ability		Grain size		Panicle node number‡		Panicle size	
Category	LQ no.	Tillering ability rating†	Level	Grain (g)	Level	Days to heading	Level	Panicle size rating§	Level
1	LQ170	4.00	Low	0.0220	Low	89	Low	7	Low
2	LQ49	2.75	Low	0.0165	Low	84	Low	11	High
3	LQ55	3.25	Low	0.0150	Low	103	High	6	Low
4	LQ267	3.50	Low	0.0185	Low	103	High	11	High
5	LQ82	3.50	Low	0.0240	High	89	Low	7	Low
6	Lemont	3.25	Low	0.0225	High	89	Low	H	High
7	LQ348	3.00	Low	0.0270	High	96	High	6	Low
8	LQ199	4.00	Low	0.0230	High	96	High	11	High
9	LQ287	5.50	High	0.0210	Low	84	Low	3	Low
10	LQ125	4.50	High	0.0150	Low	89	Low	11	High
11	LQ214	6.25	High	0.0220	Low	103	High	6	Low
12	LQ81	4.50	High	0.0180	Low	103	High	10	High
13	LQ338	5.00	High	0.0240	High	89	Low	8	Low
14	LQ248	5.25	High	0.0225	High	89	Low	11	High
15	LQ306	6.25	High	0.0225	High	110	High	3	Low
16	Teqing	6.00	High	0.0250	High	96	High	H	High

† Tillering ability rating ranged from 1 (lowest tillering ability) to 7 (highest tillering ability).
‡ Panicle node number was based on days to heading, that is, rice lines with later heading dates were rated as having more nodes.
§ Panicle size rating ranged from 1 (lowest panicle size) to 16 (highest panicle size). Lemont and Teqing were not included in the rating of the F_8 lines. However, their panicle sizes were rated as high, as their panicle sizes were greater than the mean panicle size of the F_8 lines.

ha^{-1} in 1995), during thinning (79.4 kg N ha^{-1} in 1994 only), after thinning (79.4 kg N ha^{-1}), and at panicle differentiation (79.4 kg N ha^{-1}). The permanent flood water level was maintained at 10 cm starting at fertilization following plant thinning.

Biomass samples were obtained from one of five 0.7- by 0.3-m quadrats within the inner four rows (0.7-m width by 3.9-m length) of each plot. Sampling was conducted for each rice genotype approximately once every 12 to 14 d during the entire growth period for a total of six sampling dates for the earliest maturing line to 11 sampling dates for the latest maturing line. On each sampling date, plants were dug to a depth of 27.5 cm and washed to remove adhering soil. The plant samples were then divided into (i) main plants, MP; (ii) first and second tillers, T1T2; and (iii) third and fourth tillers, T3T4.

Within each tiller group, the plant samples were subdivided into stems (culms and leaf sheaths), leaf blades, panicles, and roots. To minimize wilting and respiration during the separation of tillers and plant structures, the plant samples were kept in ice-cold water. All samples were dried at 70°C in a ventilated oven. Dry weights were obtained after 48 h or until a constant weight was obtained. The samples were then ground using a cyclone sample mill (Udy Corporation, Fort Collins, CO) with a mesh size of 0.5 mm, after which they were sealed in plastic vials and stored at 4°C until analyzed for TNC concentration.

Heading date was estimated as the number of days from sowing to the exsertion of 50% of the panicles in each plot. Minimum and maximum daily temperature, daily rainfall, and solar radiation data were obtained from the Texas A&M University Research and Extension Center, Beaumont.

TNC Determination

The TNC determination method was modified from procedures developed by Hendrix (1993) and Tarpley et al. (1993). Sulfuric acid (4 mL 5 m*M* H_2SO_4) was added to 15-mL polypropylene tubes containing 0.15 g ground samples. The tubes were then autoclaved (20 min at 103.4 kPa at 121°C) to gelatinize the starch grains, hydrolyze the fructans, disrupt the membranes, and release the sugars into solution. To break down starch into maltose and oligosaccharides, 1 mL 100 m*M* HEPES (*N*-2-hydroxyethylpiperazine-*N*'-2-ethanesulfonic acid), pH 6.9, containing 100 EU porcine pancreas α-amylase was added. These were then incubated at 38°C for 40 to 44 h and agitated twice per day. The carbohydrates in solution were separated from the structural residues 15 min after agitation by transferring 1.25 mL of the supernatant into 7-mL mini-vials. Maltose, a product of the previous step, was broken down into glucose by adding 0.25 mL 35 m*M* K_2HPO_4, 100 m*M* dithiothreitol, pH 7.5, containing 20 EU amyloglucosidase, followed by incubation for 45 min at 38°C. Absolute ethanol (4.5 mL) was added to prevent sugar adsorption to charcoal in the next step. Activated charcoal (0.1 g) was added to remove substances that could interfere with enzyme activities. The samples were then agitated and the charcoal was allowed to settle overnight while in cold storage (4°C).

The TNC content in the aliquots in the microtiter plate wells was determined by the methods of Hendrix (1993) for sucrose assay, except that the reaction mixtures were prepared by the modified method of Tarpley et al. (1993). The previous steps in sample processing had converted all TNC into sucrose, glucose, or fructose. The sucrose assay as used is designed to reduce iodonitrotetrazolium violet stoichiometrically to the hexose equivalents present in these sugars. After a 40-min incubation and consequent reduction of iodonitrotetrazolium violet absorbance at 490 nm was measured with an ELx-800 microtiter plate reader (Biotek Instruments, Inc., Winooski, VT). The content of hexose equivalents of TNC was determined by comparison with a glucose standard curve. The r^2 for a linear fit was typically 98%.

Statistical Analyses

Path analyses as described by Li (1975) were used to organize and present the causal relationships between predictor variables (leaf and stem TNC) and response variable (panicle TNC) through a path diagram. This analysis partitioned the correlation coefficient between leaf and stem TNC content (g m^{-2}) and panicle TNC content (g m^{-2}) into its components—the path coefficient which measures the direct effect of a predictor variable upon its response variable; and the indirect effect(s) of a predictor variable on the response variable through other predictor variables (Dewey and Lu, 1959). Since each cultivar reached harvest at different dates, the biomass sampling of the 15 lines did not correspond with the

same stage of phenological development. In addition to the TNC content at the harvest stage, the TNC content for each of four sampling dates prior to harvest which were chosen to represent the pre-heading, early heading, late heading, and grain hardening stages (49, 37, 26, and 15 d before harvest, respectively) was interpolated. Harvest is defined in this paper as the point when approximately 80% of grains in the panicles are straw-colored and the grains in the lower portions of the panicle are in the hard-dough stage (De Datta, 1981). The change in TNC content between successive stages was computed for each structural part. Four periods were obtained from the five stages. Within each period, path coefficients served as the estimate of the direct effects on Δ panicle TNC content caused by the changes in leaf and stem TNC content.

Analyses of variance were conducted to determine the significance of year, genotype, developmental stage (heading and harvest), tiller group, and plant structure (leaf, stem, and panicle) on rice biomass (g m^{-2}) and TNC concentration (g kg^{-1}). For dry weights (g m^{-2}) and TNC concentrations (g kg^{-1}) of plant structures, contrasts were performed between the low and high levels for the four phenotypic categories. When the field sampling did not exactly coincide with the heading date, the dry weights and TNC concentrations of plant structures at heading were interpolated. Roots were excluded from the analyses because the field root data were not separated into tiller groups. In addition, the whole plant root TNC concentration was generally low at around 10 g kg^{-1} dry weight.

RESULTS AND DISCUSSION

Seasonality of Biomass and TNC Concentration

The seasonal patterns for main plant biomass and TNC concentration for the earliest (LQ49) and latest (LQ306) heading rice lines are presented in Fig. 1 and 2. Heading for LQ49 occurred at 77 d from planting in 1994 and 78 d from planting in 1995. In contrast, LQ306 headed at 114 d from planting in 1994 and 118 d from planting in 1995. In both years, leaf dry weights of both lines increased to a maximum around heading then declined afterwards. This pattern was in general the same for all 15 genotypes. Green leaf TNC was relatively stable (compared to stem and panicle TNC) averaging 68.5 g kg^{-1} in 1994 and 48.5 g kg^{-1} in 1995 for the 15 genotypes. In both years, stem dry weights increased to a maximum just after heading in lines LQ49 and LQ306 then declined during grain filling. Published research showed that TNC accumulation in the leaf sheath and culm reaches a maximum at or before heading (Perez et al., 1971; Murata and Matsushima, 1975; Rowland-Bamford et al., 1990). In this study, stem TNC of LQ49 peaked at around heading (405.8 g kg^{-1} in 1994 and 306.0 g kg^{-1} in 1995). In comparison, other studies reported maximum carbohydrate concentrations at 300 g kg^{-1} for Lemont's leaf sheath (Andrews, 1990) and 240 g kg^{-1} for IR8's stem (Yoshida and Aha, 1968, as cited by Murata and Matsushima, 1975). There was a reaccumulation of stem TNC in LQ49 for both years during the grain hardening stage until harvest, with the 1994 stem TNC at harvest being even greater than that during heading. Saitoh et al. (1991) and Akita (1995) stated that high-yielding cultivars exhibit reaccumulation of TNC in leaf sheath and culm at harvest. Andrews (1990) and Turner and Jund (1993) explained TNC reaccumulation as characteristic of rice lines with improved ratoon potential. However, in this study, although LQ49 was the earliest maturing line, it was a low-yielding line

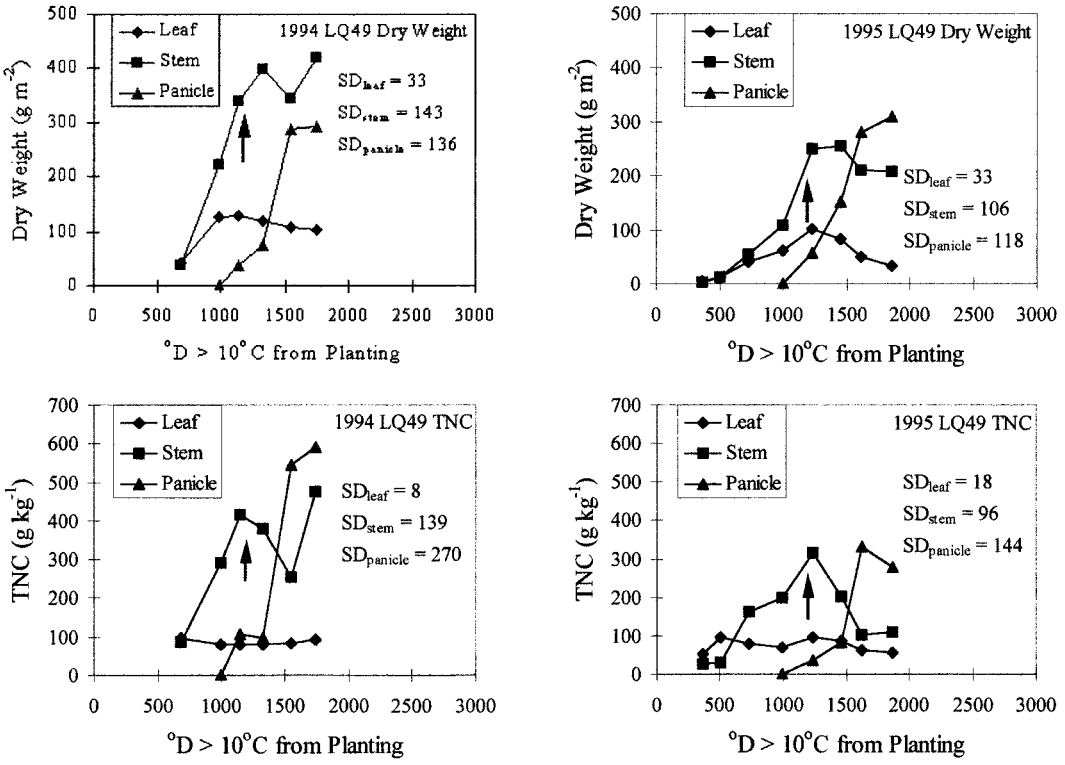


Fig. 1. Dry weight and TNC concentration of leaves, stems and panicles of rice genotype LQ49 main plants in 1994 and 1995. Arrows indicate heading date.

ranking 13th among the 15 lines. Hence, TNC reaccumulation indicates either a limitation in translocation of assimilates into the grain or a limited grain storage capacity (Murata and Matsushima, 1975). Other genotypes that exhibited reaccumulation of TNC were LQ287, LQ125, LQ214, LQ81, and Teqing.

The seasonal pattern for stem TNC concentration in LQ306 was quite different between 1994 and 1995. In 1994, TNC peaked around panicle differentiation and generally declined afterwards. In 1995, decreases in stem TNC coincided with extreme daily maximum temperatures. During the vegetative stage, stem TNC decreased sharply from the third sampling date (14 June) to the fourth sampling date (28 June), i.e., from 287.9 to 17.9 g kg^{-1}. Between these sampling dates, there were five consecutive days (24–28 June) with maximum temperatures ≥35°C. These high temperatures may have increased maintenance respiration causing an increased loss in assimilates (Yamamoto, 1954, as cited by Murata and Matsushima, 1975; Murata, 1964; Yoshida, 1981). Except for LQ49 and LQ287, which were the two earliest lines, similar trends were observed for the other 12 genotypes wherein stem TNC decreased with high daily maximum temperatures.

Panicle dry weight increased rapidly for each of the 15 genotypes. As illustrated for LQ49 and LQ306, panicle weight was much greater in 1994 than in 1995 (Fig. 1 and 2). Panicle TNC concentration decreases around heading because of the increased respiration of anthesis (Cock and Yoshida, 1972), then increases rapidly during grain filling. The rate of increase in panicle TNC was higher in 1994 (37.5 g kg^{-1} d^{-1} for LQ49 and 37.2 g kg^{-1} d^{-1} for LQ306) than in 1995 (27.5 g kg^{-1} d^{-1} for LQ49 and 13.8 g kg^{-1} d^{-1} for LQ306). This compares with 31.5 g kg^{-1} d^{-1} in 1994 and 29.6 g kg^{-1} d^{-1} in 1995 when averaged across genotypes. Panicle TNC at harvest for LQ49 was 589.66 g kg^{-1} in 1994 and 277.69 g kg^{-1} in 1995, while for LQ306 it was 603.60 g kg^{-1} in 1994 and 452.44 g kg^{-1} in 1995. When averaged across genotypes, the panicle TNC concentration at harvest was 527.6 g kg^{-1} in 1994 and 405.2 g kg^{-1} in 1995. The decrease in panicle TNC at harvest has also been observed in other studies (Andrews, 1990).

Effects on Panicle TNC

The path analyses showed that changes in stem TNC content (g m^{-2}) had a negative direct effect on panicle TNC content during the early-heading to late-heading period and during the late-heading to grain hardening period (Fig. 3). Path coefficients for the direct effect of Δ stem TNC on Δ panicle TNC were −0.46 ($P = 0.018$) during the early-heading to late-heading period and −0.59 ($P = 0.002$) during the late-heading to grain hardening period. This suggests that the decrease in stem TNC content was caused by translocation of the accumulated stem TNC to panicles during these periods. The indirect effect of Δ stem TNC on Δ panicle TNC through Δ leaf TNC content were near zero at −0.002 for the early-heading to late-heading period and −0.010 for the late heading to grain hardening period.

There were no significant direct effects by either Δ

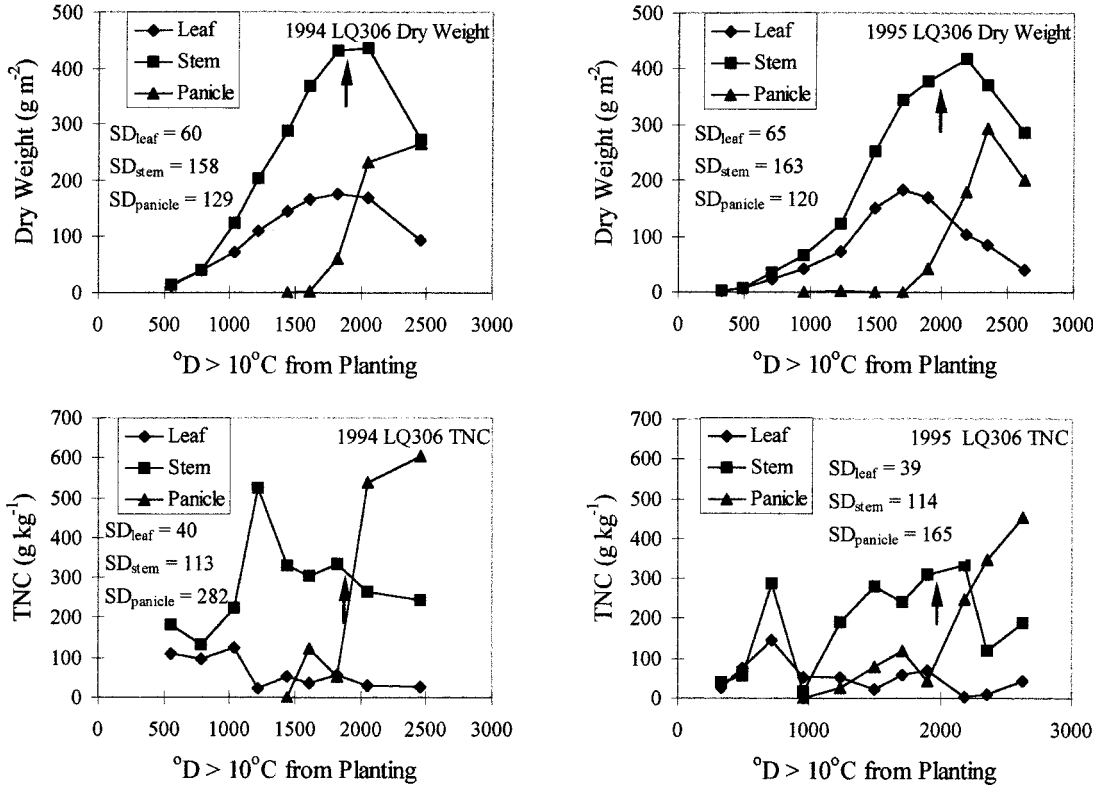
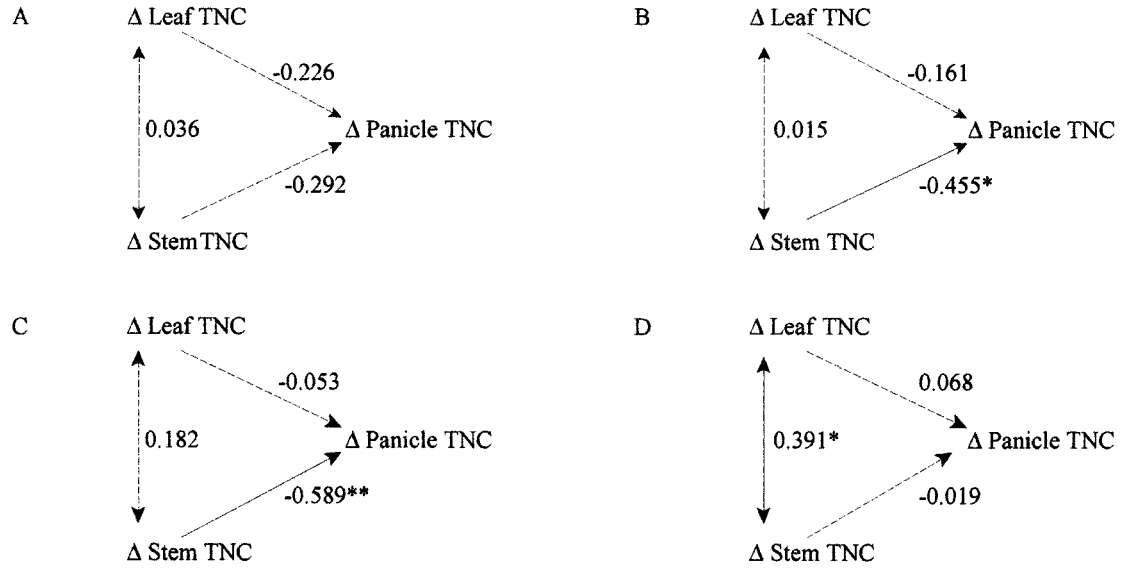


Fig. 2. Dry weight and TNC concentration of leaves, stems and panicles or rice genotype LQ306 main plants in 1994 and 1995. Arrows indicate heading date.



*,** Significant at the 0.05, and 0.01 probability levels, respectively.

Fig. 3. Correlation (double-arrowheaded lines) between Δ leaf and Δ stem TNC content and their direct effects (single-arrowheaded lines) on Δ panicle TNC of rice during the (A) pre-heading to early heading period, (B) early heading to late heading period, (C) late heading to grain hardening period, and (D) grain hardening to harvest period. Non-solid lines indicate non-significant correlation or path coefficients.

leaf or Δ stem TNC during the preheading to early-heading period and the grain hardening to harvest period. Neither was there a significant direct effect by Δ leaf TNC on Δ panicle TNC throughout the four periods.

Contributors to Plant Structure Dry Weight and TNC

The diversity of rice genotypes achieved by selecting the low and high genotypes for tillering ability, grain weight, panicle node number, and panicle size was reflected in the analysis of variance for dry weight. All main effects (year, genotype, stage, tiller group, and plant structure) and most interactions significantly affected dry weight. Tiller group, plant structure, and stage × plant structure interactions accounted for 78.4% of the total variation for dry weight.

The factors that had significant effects on TNC concentration were year (Y); genotype (G); developmental stage (S); plant structure (P); and Y × G, G × S, Y × P, G × P, S × P, Y × S × P, and G × S × P interactions. Tiller group did not affect TNC concentration as a main effect nor as part of any interaction effect, indicating that TNC concentration did not differ among main plants or tillers even though tillers differed in dry weight. Stage × plant structure interaction contributed the largest to TNC variation. The significant G × S × P interaction, which primarily reflected differences among genotypes in the stem TNC decline and panicle TNC increase with developmental stage, indicated the potential for selection of rice lines with high TNC concentration in stems at heading. The TNC accumulated in stems at heading is one of two major contributors to grain TNC at harvest, the other being photosynthates produced after heading (Sato and Inaba, 1976). Table 2 shows the genotype means for dry weight and TNC concentration of stems at heading and of panicles at harvest.

Linear contrasts were conducted between the low- and high-genotypes of the phenotype classes. The variables examined were leaf, stem, and panicle dry weights (g m^{-2}), and TNC (g kg^{-1}) at heading and at harvest (Table 3 and 4). The contrasts showed that abundantly (high) tillering genotypes had greater leaf and stem dry weights at heading and at harvest. High tillering genotypes also had greater panicle weights at heading and harvest but these differences were not significant. The high grain weight genotypes had greater leaf weights at heading, smaller leaf and stem weights at harvest, and

Table 2. TNC concentration and dry weight averaged over years of stems at heading and panicles at harvest of 15 rice genotypes.

Rice genotype	Stems at heading		Panicles at harvest	
	TNC	Dry weight	TNC	Dry weight
	g kg^{-1}	g m^{-2}	g kg^{-1}	g m^{-2}
LQ170	292.3ab†	155.4g	462.9ab	208.2bc
LQ49	284.1ab	176.7efg	492.4ab	193.2bc
LQ55	198.3bc	205.8def	316.2b	202.8bc
LQ267	290.8ab	300.5a	403.4b	201.6bc
LQ82	257.4abc	167.8fg	461.4ab	173.9bc
Lemont	330.2a	172.9fg	455.4ab	175.0bc
LQ348	340.1a	310.0a	524.4ab	210.7bc
LQ199	256.6abc	226.4bcd	465.0ab	296.5a
LQ287	258.2abc	170.3fg	581.2a	211.0bc
LQ125	333.8a	229.6bcd	299.4b	184.4bc
LQ214	288.6ab	221.1cde	465.7ab	163.8c
LQ81	172.9bc	290.9a	533.4ab	220.9b
LQ248	142.9c	176.2efg	559.2ab	199.0b
LQ306	267.5abc	264.4abc	507.4ab	171.0c
Teqing	259.8abc	273.3ab	468.6ab	318.4a

† Means within the same column followed by the same letter are not significantly different at the 0.05 probability level according to Tukey's HSD.

Table 3. Dry weight averaged over years of leaves, stems, and panicles during heading and harvest of the low (L) and high (H) grouping of rice genotypes determined on the basis of tillering ability, grain weight, panicle node number, and panicle size.

		Mean dry weight					
		Heading			Harvest		
Genotype groups		Leaf	Stem	Panicle	Leaf	Stem	Panicle
		g m^{-2}					
Tillering ability group	L	81.6b†	212.6b	37.4	30.6b	173.1b	205.7
	H	89.6a	225.7a	47.8	43.1a	174.8a	212.6
Grain weight group	L	81.7b	219.3	37.1	43.5a	202.2a	196.2b
	H	89.8a	219.0	48.1	30.3b	145.8b	222.1a
Panicle node number group	L	71.4b	177.3b	38.3b	32.9b	138.8b	194.6b
	H	99.8a	260.9a	46.8a	40.8a	209.1a	223.7a
Panicle size group	L	84.2	208.2b	42.0	35.7	157.9b	196.7b
	H	87.0	230.0a	43.2	38.1	190.1a	221.6a

† Within each contrast between L and H groups of each physiological stage and structural part, means followed by different letters are statistically different at the 0.05 probability level.

higher panicle weights at harvest. Among the four genotype groupings, only panicle node number contributed significantly to variation in all plant structures at both stages. Greater leaf, stem, and panicle weights in the high panicle node genotypes could be attributed to relatively more nodes providing more positions for leaves, internodes, tillers, and panicles. The high panicle size genotypes had significantly greater stem weights at heading, and greater stem and panicle weights at harvest. These contrasts indicated that in addition to the genotype traits of high grain weight and high panicle size, both of which are yield components, high panicle node genotypes achieve high panicle weights at harvest.

Significantly higher TNC concentrations in stems at heading and panicles at harvest were observed in the high tillering genotypes. The high grain weight genotypes had significantly lower panicle TNC at heading, lower stem TNC at harvest, and higher panicle TNC at harvest. Since the low grain weight genotypes had significantly higher TNC concentrations in their stems at harvest, this indicated that either translocation of assimilates into the grain or storage capacity of the grain was limiting (Murata and Matsushima, 1975). Hence, the minimization of limitations in either translocation of assimilates or storage capacity requires for the selection of high grain weight genotypes.

The significance of the year main effect on TNC concentration partly explained the low rice grain yields attained in 1995. The decrease ($P < 0.001$) in plant dry weight from 148.4 g m^{-2} in 1994 to 108.1 g m^{-2} in 1995 was reflected by the decrease ($P < 0.001$) in TNC concentration from 192.3 g kg^{-1} in 1994 to 156.0 g kg^{-1} in 1995. Total nonstructural concentrations of leaves, stems, and panicles at heading and at harvest were generally lower in 1995 than in 1994, with the exception of stems at harvest. Sato and Inaba (1976) observed that when rice was grown at 35°C, the translocation rate of assimilates to grain declined and the grain filling period shortened resulting in TNC concentrations in stems that were relatively higher than in rice grown at 25°C. High daily maximum temperatures during July and August 1995 have been suggested as the cause for the dry weight and yield decreases (Wilson et al., 1996). In 1994, daily maximum temperatures exceeded 35°C for 1 d in July and 3 d in August, while in 1995, the daily maximum temperatures exceeded 35°C for 13 d in July and for 12 d in August. High temperatures increase maintenance respiration causing an increased loss of assimilates (Yamamoto, 1954, as cited by Murata and Matsushima, 1975; Murata, 1964; Yoshida, 1981).

Correlation analysis was conducted to determine whether high stem TNC at heading was due to relatively lower number of few spikelets or grains available to take up the TNC. The results indicated that stem TNC at heading was not significantly correlated with either number of spikelets at heading or number of grains at harvest during 1994, 1995, and the combined 1994-1995 data. This indicated that stem TNC at heading had no

Table 4. TNC concentration averaged over years of leaves, stems, and panicles during heading and harvest of the low (L) and high (H) grouping of rice genotypes determined on the basis of tillering ability, grain weight, panicle node number, and panicle size.

		TNC concentration					
		Heading			Harvest		
Genotype groups		Leaf	Stem	Panicle	Leaf	Stem	Panicle
		g kg^{-1}					
Tillering ability group	L	44.4	279.5b†	84.5	35.7	125.5	445.9b
	H	47.3	286.9a	70.9	45.5	150.0	480.7a
Grain weight group	L	49.0	263.2	100.2a	48.8	182.5a	438.7b
	H	42.7	303.2	55.1b	32.4	93.0b	487.9a
Panicle node number group	L	43.9	308.7	80.4	40.3	121.4	466.7
	H	47.8	257.7	74.9	40.9	154.1	459.9
Panicle size group	L	31.3	309.2	68.2	27.4	142.4	474.2
	H	60.4	257.2	87.1	57.8	133.1	452.4

† Within each contrast between L and H groups of each physiological stage and structural part, means followed by different letters are statistically different at the 0.05 probability level.

significant linear relationship between either the number of spikelets at heading and the number of fertile spikelets that developed into grains at harvest.

Sato and Inaba (1976) reported that the panicle to straw ratios for dry weight and TNC content were lower at high temperature (35°C maximum, 30°C minimum) than at favorable temperatures. In their study, panicle to straw TNC content ratios were 11.3 at favorable temperature and 4.7 at high temperature, while panicle to straw dry weights ratios were 1.2 at favorable temperature and 0.8 at high temperature. A similar trend was shown in this study wherein panicle-to-straw ratios were lower in 1995 which was relatively hotter during July and August in 1995 than in 1994. The mean panicle to straw ratio for TNC content of main plants at harvest was 15.6 in 1994 and 5.7 in 1995, while the mean panicle to straw ratio for dry weight was 1.35 in 1994 and 0.94 in 1995.

Wada (1969) estimated the ratio of shoot TNC content at heading to grain TNC content at harvest to be about 0.1 to 0.4. Since this study measured panicle TNC instead of grain TNC, the ratio of stem TNC content at heading to the panicle TNC content (which is the TNC content of grains and panicle branches) at harvest is expected to be greater. Nevertheless, applying this ratio to the TNC contents of main plants resulted in a 1994 mean ratio of 0.61 and a 1995 mean ratio of 1.04. This indicated the possibility that the 1995 growing season relied heavily on the accumulated stem TNC at heading which was translocated into the panicles. This implies the importance of stem TNC as a potential TNC buffer during grain filling when the weather is unfavorable, such as high maximum daily temperature. Only three genotypes had ratios that were lower in 1995 than in 1994: LQ170 (0.56 in 1994, and 0.50 in 1995), LQ49 (0.92 and 0.87), and Lemont (0.73 and 0.55).

CONCLUSIONS

The importance of the amount of TNC that accumulated in the stems at heading that was translocated to panicles after heading was established through the path analyses of TNC partitioning in rice. The significant negative direct effects of Δ stem TNC on Δ panicle TNC content were −0.46 for the early- to late-heading period and −0.59 for the late-heading to grain hardening period. The significant genotype × developmental stage × plant structure interaction indicated the potential for selection of genotypes with high TNC concentration in stems at heading. The low grain weight genotypes had higher stem TNC concentrations at harvest, which suggested the selection of higher grain weight genotypes to maximize translocation of stem TNC to the panicle and also to maximize grain storage capacity.

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NOTES

DISTRIBUTION OF BUFFALOGRASS POLYPLOID VARIATION IN THE SOUTHERN GREAT PLAINS

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ABSTRACT

Buffalograss [*Buchloë dactyloides* (Nutt.) Engelm.] is indigenous to the short-grass prairies of North America and is a polyploid series of diploid, tetraploid, and hexaploid individuals. It has a base chromosome number of $x = 10$. The distribution pattern of these ploidy levels is not well-defined, especially in the southern Great Plains. We predicted the ploidy levels of 273 buffalograsses from the southern Great Plains of North America using flow cytometry to measure cellular DNA content. The buffalograss accessions were grouped into four distinct ploidy level groups. Very few diploid accessions were collected (2.6% of the collection), and all were found in northwest Texas and eastern New Mexico. Tetraploid accessions (23% of the collection) were found exclusively in the western regions of the southern Great Plains. Hexaploids were the most prevalent ploidy level, representing 73% of the collection and found throughout the collection area. Pentaploid accessions were also found in field sites (1.8% of the collection). No clear pattern of adaptation for ploidy levels is apparent from these data. In other collections, cold hardiness appears associated with higher ploidy levels, but this pattern is not apparent in the southern Great Plains.

Buffalograss is a warm-season perennial grass that has been the subject of substantial plant breeding and development work in recent years for use in forage and low-maintenance turfgrass areas. Buffalograss is a low-growing, sod-forming species with tolerance to drought, diseases, and wide temperature extremes (Savage, 1934; Wenger, 1943). The most recent breeding work has been for low-water use landscapes where buffalograss maintains better turfgrass quality than many cool-season grasses (Riordan et al., 1993).

Buffalograss is native to the North American Great Plains and is distributed north to south from Canada to Mexico and west to east from the eastern slope of the Rocky Mountains to the Mississippi Valley (Fig. 1). It is the dominant species in the short-grass prairie—the driest part of the Great Plains (Fig. 1).

Like many other prairie grasses, buffalograss comprises a polyploid series. The base chromosome number is $x = 10$ with diploid, tetraploid, and hexaploid plants reported. Morphologically, all three ploidy levels are indistinguishable. No characteristics have been found to consistently identify between them. All three ploidy levels have been documented in Mexico (Reeder, 1971) but diploids have been reported only in central Mexico and southeastern Texas (Huff et al., 1993). Hexaploids can be found throughout the Great Plains (Huff et al., 1993; Johnson et al., 1998). Buffalograss plants collected from Kansas, Nebraska, and Colorado are primarily hexaploids and tetraploids (Johnson et al., 1998). Tetraploids are also thought to be prevalent in the westernmost regions (Huff et al., 1993). However, the actual distribution of the ploidy levels is not well-defined.

In this research, we studied a collection of buffalograsses collected from the southern Great Plains for distribution of ploidy levels, and report correlations with potential adaptational traits.

Materials and Methods

During 1994 and 1995, a systematic collection of 273 buffalograss plants was made during seven trips in the southern Great Plains. Each trip began and ended in Lubbock, TX. Grasses were collected from 242 sites that averaged 55 km apart, ranging from 1.6 to 160 km apart. At each collection site, a plant was selected based on color, but was representative of the population at that location. Plant color was involved in the collection process in order to build a breeding population for turfgrass variety improvement work. If two or more distinct populations were present at the collection site, each

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